(*American Naturalist Extra, November, 1886.*)

IS LITTORINA LITOREA INTRODUCED OR INDIGENOUS?

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IT is now nearly thirty years since *Littorina litorea* (Linn.), the English periwinkle, was first reported from American waters, but the question as to whether it has been recently introduced or was an original inhabitant of our shores is still unsettled. This mollusk, though not known by naturalists to occur upon the coast of Acadia and New England previous to its discovery at Halifax in 1857 by John Willis, is at present very abundant from the Gulf of St. Lawrence to Connecticut.

Professor Verrill (Amer. Jour. Sci., iii, IV, p. 133, 1874) says of it: "It has been supposed by several writers that this shell (*L. litorea*) has been recently and accidentally introduced from Europe; but Dr. Dawson informs me that he collected it more than thirty years ago in the Gulf of St. Lawrence. It is abundant at Halifax, and we have other specimens from Kennebunkport, Me., Hampton Beach, N. H., and Provincetown, Mass. There is really no sufficient evidence that it was not an inhabitant of our shores before the advent of Europeans, but local in its habitats. It may have become more diffused in recent times by commerce, or it may have been overlooked formerly by collectors."

The causes determining the geographical distribution of animal and plant life are a subject of the greatest importance to naturalists, and any contribution to it has its value. So peculiar and

interesting are the known facts in regard to the distribution and spread in America of the shell we are considering, that an inquiry into the nature of these facts, and a search for an explanation for them becomes a matter of more than special importance. The value of the settlement of the question as to whether *Littorina litorea* has been introduced in recent times or is a native of America, is not limited to the settlement of this fact only. It has a broader value as well, inasmuch as it has a bearing upon the science of the distribution of animals.

It must be remembered that no species of animal or plant can, in the strict sense of the word, be indigenous to both Europe and America. If such were the case it would be necessary to suppose that the two independent lines of descent, either from a common near or remote ancestor, culminating in the species, had followed precisely identical courses of development. The latter would require precisely identical conditions of environment—and such we know would not exist upon two separate continents. Hence a shell which is common to two continents must in some way have been introduced from one to another. It may be introduced by the agency of man, or by purely natural and physical causes, such as ocean currents, etc. For want of a better term the word *indigenous* has been used in the present paper to apply to a species introduced in past time by *natural* agencies and now thoroughly established as a resident.

Such a species is our so-called "native periwinkle," *Littorina palliata* (Say). It is common to Europe, Greenland and America, and has existed for a long time in all three countries, being found fossil in the Post-pliocene of all of them. It will be presently shown that this shell was probably introduced from the continent in which it *originated* to the other by way of Greenland and Iceland, and by strictly natural agencies. We therefore speak of it as indigenous to America, though whether its descent from its parent species took place here or in Europe we are unable to say. But we hope to be able to show that *Littorina litorea* did not exist in America until introduced from Europe by man, and that since the beginning of the present century.

Mr. John Willis, who was the first to announce its discovery in America (Trans. Nova Scotia Inst. Nat. Sci., Vol. 1), found it at Halifax in 1857. He considered it to be indigenous to Nova Scotia chiefly for the reason that "some of the oldest inhabitants

have assured me that they have 'often picked the periwinkle, the same as the English one,' on the shores contiguous to Halifax when they were only school-boys."

The only other evidence that has been found to show that the shell was known in Nova Scotia, previous to 1857, comes in a private letter to the writer from Mr. E. Gilpin, of Halifax. He says: "Historical evidence in the shape of old English settlers shows it to have been known in the province as far back as 1800."

How much reliance can be placed upon the unscientific evidence of old settlers is a question; but granting that they did not confound it with the native form, and that they actually saw it previous to 1857, nothing more is proved than that the shell existed in Nova Scotia some years before Willis found it. Similarly it may be said of the fact that Dr. Dawson "collected it more than thirty years ago in the Gulf of St. Lawrence," that it proves (if granted) only that the shell was to be found there earlier than any published record shows. Or it may be that, if introduced, it was introduced at more than one point.

It is somewhat remarkable, however, that, as will be shown farther on, no other collector found this conspicuous shell in the gulf until after 1870, although Dr. Dawson must have found it at least as early as 1844. We know that it increases with great rapidity wherever introduced. Why then, if it existed there, did it not increase sufficiently to enable some other collector to find it? None of the lists of Bell, Whiteaves or Dr. Dawson himself mention it until after 1870. It is to be regretted that we have not some record of Dr. Dawson's discovery of the shell so far back, besides the note by Professor Verrill who doubtless writes from memory.

If this shell be indigenous to our shores, it must have been confined, previous to say 1850, exclusively to the Nova Scotia coast. That this must be so is shown as well by other facts as by the many lists we have of New England and Gulf of St. Lawrence shells, all of which mention the native periwinkles, *L. palliata*, *L. rudis*,[1] *L. tenebrosa*,[1] while *L. litorea* never appears. That the latter could have been present but "overlooked by collectors" is altogether out of the question. It is a much larger and more conspicuous shell than the native forms, has the same habitats, and wherever it occurs at all occurs abundantly.

[1] For convenience we will consider these two to be distinct species, although they are probably varieties of the same species.

Among the many lists of New England shells which might be named, the following have been selected:

Gould's "Invertebrata of Mass.," 1st ed. (1841), mentions *L. palliata, rudis* and *tenebrosa* but not *litorea.*

Mighel's list of the shells of Maine[1] (1843) mentions *L. palliata, rudis* and *tenebrosa* as occurring "in the greatest profusion," but *L. litorea* is not in the list.

Reed's "Catalogue of the Shells of Mass."[2] (1845) mentions the same three but not *litorea.*

Russell's "Retrospect of some of the Shells found in Essex county, Mass."[3] (1851), mentions the same three but not *litorea.*

Tuft's "List of Shells collected at Swampscott Lynn and vicinity" (1853) mentions the same three as abundant, but not *litorea.*

Stimpson's "List of the marine Invertebrates of Grand Manan" (1854) mentions *L. palliata* (= *L. littoralis*) and *L. rudis*, but not *L. litorea.*

Tuft's "Catalogue of Shells in the State cabinet [of Mass.]" (1859) mentions the same three but not *litorea.*

Nor has it been reported until quite recently from the Gulf of St. Lawrence.

Dr. Dawson's "A week in Gaspé"[4] (1858) mentions *L. rudis* and *L. palliata*, but not *L. litorea.* If Dr. Dawson found it in the Gulf of Lawrence "thirty years ago," it must have been at some other point.

Robert Bell's "List of the Mollusca of Eastern Canada"[5] (1859) mentions *L. palliata* only.

J. F. Whiteaves' "On the marine Mollusca of Eastern Canada"[6] (1869) mentions *L. palliata* (*littoralis*), *L. rudis* and *L. tenebrosa*, but not *L. litorea.*

Although the evidence of these lists is only negative, their combined force is so strong (even had we no other evidence) that they practically prove that the shell did not exist upon the New England coast, and probably not in the Gulf of St. Lawrence, previous to the middle of the present century. Since 1857 its spread has been phenomenally rapid. A paper, by A. F. Gray, in Science News for 1879, gives many localities which it had come to inhabit upon the New England coast, and the known facts of its spread are thus summarized by Professor Verrill:[7]

"It is well known to American conchologists that this common European species has become well established upon the New England coast within ten or twelve years, appearing first upon

[1] Boston Jour. Nat. Hist., IV.

[2] See for this as well as other lists, Binney's "Bibliography of American Conchology," Smithsonian, Vol. I.

[3] Jour. Essex county Nat. Hist. Soc., I.

[4] Can. Nat., III, 321.

[5] Can. Nat., IV, 197.

[6] Can. Nat., ii, IV. 48. See also Can. Nat., ii, IV, 270.

[7] Am. Jour. Sci., iii, XX, 251.

the coast of Maine about 1868; Dr. Dawson, however, states that he collected it on the shores of Nova Scotia at a much earlier date. I wish at present merely to put on record some additional data as to its recent progress along the coast. In 1873 it was collected in abundance at Saco, Maine, by the U. S. Fish Commission, and was found sparingly at Peake's island, Casco bay. In 1872 it was very rare at Provincetown, Mass., but in 1875 it was common there. In 1875 it was collected by the writer at Barnstable, Mass., on the shores of Cape Cod bay, in large quantities. In 1879 it had become exceedingly abundant at Provincetown. In 1875 our parties found two specimens only on the southern shores of Cape Cod, at Wood's Holl, but in 1876 it was found to be common there, and is now very abundant. The first specimen found so far westward as New Haven was obtained by Professor S. I. Smith during the past winter ['79–80]. Other solitary specimens have since been obtained here by E. A. Andrews and by J. H. Emerton. It is at present exceedingly abundant at Newport, R. I."

It is spreading into the Gulf of St. Lawrence, too, finding probably a congenial habitat in the warmer water of Northumberland straits, which contain so many southern forms. J. F. Whiteaves found it at Souris and Charlottetown, P. E. I., in 1873.[1]

Do not these facts afford an exceedingly strong argument that the shell has been introduced? Its rapid increase southward shows that a favorable habitat was there waiting for it—a much more favorable one than the Nova Scotia coast. The conditions which determine its spread were here at work a century ago, but it was not found anywhere in New England.

As has already been pointed out, no species of animal or plant can be truly indigenous to the two continents. It must either have originated in one and spread to the other, or it must have originated at some other point and spread to both. A shell such as we are considering, which is at present common to both continents must either have been introduced from one to the other by man's agency, or by purely natural means. If it can be shown that the natural means did not operate in this case, it would prove that man must have introduced it; and the stronger the probability of the former, the stronger will be that of the latter.

Winds or the agency of birds, so active in the distribution of plants, could hardly operate upon a shell or its young. Ocean currents seem to be the only method of conveyance. But by no means could either *L. litorea* or *L. palliata* directly cross the At-

[1] Report on deep-sea dredging operations in the Gulf of St. Lawrence.

lantic in such a way—they must have come, if they came by natural means at all, by way of Iceland, Greenland and Labrador.

This we find actually was the case with *L. palliata*. Where it originated the writer does not know, nor does it matter in the present connection, but certain it is that it is now common to England,[1] Greenland,[2] Labrador,[3] Acadia and New England. And not only does it exist in these places now, but it has for a long time past, for it is found fossil in Post-pliocene deposits in England, in Southern Greenland[3] (*L. grönlandica* = *L. palliata*) and in Canada, though not actually in Acadia. Dawson reports it from the Post-pliocene of Gaspé,[4] and Lyell from Beauport.[5] We may hence conclude that *L. palliata* is, in the sense in which we have used the word, indigenous to America.

But as to *L. litorea*, not only does the latest and best list of Greenland shells[2] make no mention of its occurrence there, nor does Packard in a list of the shells of Labrador[3] (though he mentions *L. palliata* and *L. rudis* as "abundant" and "not uncommon"), but no trace of it has as yet been reported from any Post-pliocene deposits of Greenland, Labrador, Canada or New England. It is a shell much more likely to be preserved in such deposits than *L. palliata*, being much larger and stouter—though neither, from their rock-loving nature, stand as much chance of being preserved as sand or mud-inhabiting species. All of these facts tend to show that *L. litorea* was not introduced from one continent to the other either at the same time or by the same means as *L. palliata*, and that if by any unknown agency whatsoever *L. litorea* had reached America, it must have been confined to Nova Scotia alone until the middle of the present century.

But we have another source of information about the shells which lived upon our coast before the advent of the Europeans. In the Indian shell-heaps along the coast of Maine and New Brunswick, most of the edible mollusks of the coast are found among the heaps of clam-shells. Dr. Wyman reports[6] that in a shell-heap at Crouch's cove, Casco bay, Maine, *Littorina palliata*

[1] Forbes and Hanley's British Mollusca, Vol. III.
[2] Manual and instructions for the Arctic expedition. London, 1876.
[3] Packard, Mem. Bost. Nat. Hist. Soc., Vol. I.
[4] Can. Nat., II, 408.
[5] Can. Nat., I, 345.
[6] AM. NAT., Vol. I, No. II, 1868.

was found along with such species as *Purpura lapillus*, *Natica heros*, *Buccinum undatum*, *Nassa obsoleta*, *Nassa trivittata*, etc., but he makes no mention of *L. litorea*. Mr. G. F. Matthew, in his account[1] of investigations into an undisturbed shell-heap on the shore of Passamaquoddy bay, New Brunswick, after mentioning the occurrence of several littoral species, says: "The rock periwinkle (*Littorina rudis*) is occasionally found * * * but the common European periwinkle (*Littorina litorea*), now so common on this coast, is entirely wanting." In a private letter to the writer the same gentleman says: "I have seen no trace of *L. litorea* in any shell-heap." That the Indians would have collected the smaller native periwinkle and other small littoral species, and not the larger English one, were the latter present, is inconceivable, no matter whether the former had been collected for food or only accidentally introduced into the shell-heaps. The same causes should have introduced *L. litorea* if it had existed at these places. Again the conclusion is forced upon us that if the shell existed in America at the time of the formation of the shell-heaps, it must have been confined to Nova Scotia. We have no published lists of shells from the Nova Scotia shell-heaps, nor has the writer been able to find by private inquiry any satisfactory account of them.

All of the facts that we have so far mentioned in connection with this shell show that if it existed at all in America previous to the present century, it must have been confined to the coast of Nova Scotia. There are other general considerations which show that in all probability it did not exist there. One of these we have already mentioned—the fact that it was not introduced in the same way as *L. palliata*, by way of Greenland, and therefore was probably not naturally introduced into America at all.

Many undoubtedly European species of both animals and plant could be named which, upon their artificial or accidental introduction into this country, have driven out and well-nigh exterminated closely-allied native species. Everywhere upon the coast of Nova Scotia as well as that of the rest of Acadia and New England, *L. litorea* is doing precisely this, driving out the native *L. palliata*. Everywhere the native form gives way before it and becomes rare, just in proportion as the English form becomes abundant. This fact of itself gives us strong *a priori* grounds

[1] Bull. N. B. Nat. Hist. Soc., III, 1884.

for believing the shell to have been recently and accidentally introduced, but it acquires additional force taken in connection with other facts which point to the same conclusion.

But granting for a moment that the shell did exist in Nova Scotia previous to this century—where it must have been confined if it was in America at all—what an anomalous condition of life we have. At present, as we follow its progress southward, we find it growing more and more abundant. The writer has very frequently noticed its distribution on the Southern New Brunswick coast, but it there occurs in nothing like the profusion in which he has seen it at Nahant, Mass., or Newport, R. I. In these two places, and they are like other localities in these two States in this respect, it literally covers the rocks, the native species becoming comparatively rare. What is the meaning of the fact that it becomes more abundant southward? Can it mean anything else than that (within certain limits) as it goes south it meets with a more and more congenial habitat? If this be so, and we can see no other conclusion, it shows that *L. litorea* thrives better in warmer water than that of the coasts of Nova Scotia and New Brunswick, and therefore that the natural home of the species, or the place where it originated was in warmer water than that of Acadia. This conclusion is strengthened by the fact of its non-occurrence in Greenland or Labrador, to both of which places it should have been carried by the same agencies which took *L. palliata* there. The latter is certainly a more northern species than the former, and it may be that the conditions of life in these two places are altogether unsuited to the more southern *L. litorea*, in which case it could certainly not have been carried from one continent the other by way of Greenland. *If* then *L. litorea* existed upon the Nova Scotia coast as (in the sense in which we are using the word) an indigenous species, it was existing without spreading under comparatively unfavorable conditions of temperature, etc., while favorable conditions were waiting for it not far to the southward. Surely the agencies which took it from one continent to the other (if naturally introduced) could have carried it to the New England coast. Is it not more natural to suppose, what so many of the facts indicate, that the warmer waters in which it thrives the best are like those of its home, and that its home is in the waters of the English coast, which we know to be so much warmer than those of Nova Scotia?

But again, what is the meaning of its wonderfully rapid spread, and why, if it existed in Nova Scotia previous to say 1850, did it not begin to spread before? Its spreading as rapidly as it has, shows that it was only waiting for the opportunity to take advantage of it, but why, if it is indigenous, did it not begin to spread sooner? Surely the same causes which have carried it south since 1850 were in operation before. If they were natural, such as currents, etc., they certainly have been present substantially unchanged for centuries. Professor Verrill suggests that it may have existed formerly in Nova Scotia, but have "become more diffused in recent times by commerce." But surely there was commerce between Nova Scotia and New England before 1868 (in which year it was first reported from Maine), and enough of it to satisfy the most exacting demands of this theory. In all probability the rapid diffusion of the shell since 1857 is in a measure due to both of these causes, but the fact that they did not have a like effect before, seems very strongly to show that the shell was not in Nova Scotia for them to spread. The waters which bathe the Atlantic coast of Nova Scotia are carried by the strong Fundy tides across to the New Brunswick and Maine coasts, and if currents had anything to do with carrying *L. palliata* from one continent to Greenland and thence to the other, it should have carried the free-swimming embryos of its ally, *L. litorea*, from the Nova Scotia to the New England coast.

But granting again for a moment that *L. litorea* has existed in Nova Scotia for an indefinitely long time as an indigenous species, we have it existing under conditions very different from those in which it thrives in England, having, as has been shown, no connection with the latter, and yet retaining its specific identity. It is possible for a species to keep its identity in widely separated localities, where the conditions of life are not precisely the same, only by a continuous intercourse between the different localities. This is in all probability the case with *L. palliata*, for we find it ranging freely around the North Atlantic in England, Greenland, Labrador, Acadia and New England, and the agencies which carried it from one land to the other have in all probability been in operation ever since. But with *L. litorea* the case is different; if it existed in Nova Scotia it must have been cut off from all communication with England, and that it should retain its

[1] We have found no list of the shells of Iceland.

specific identity under such conditions is altogether inconceivable.

We have not been able to present any *direct* proof that *L. litorea* did not exist in Nova Scotia before the present century. The testimony of the numerous lists (by independent observers, who could not have overlooked the shell had it been present) of shells on the coast of New England and New Brunswick in none of which occurs any mention of *L. litorea*, the testimony of its absence from the Post-pliocene deposits of other parts of Canada where *L. palliata* (along with which it always exists) has been found, the testimony of the Indian shell-heaps, into which it would certainly have been carried by the same means or for the same purpose as was *L. palliata*, all of these combined afford almost absolute proof that the shell did not exist on the Atlantic coast of America outside of Nova Scotia. If these same tests could be applied directly to Nova Scotia the question would be settled as to whether it occurred there. An early list of the shells of that Province, or careful investigations into its Post-pliocene deposits and Indian shell-heaps, would practically remove all doubt one way or the other. But the former does not exist and the latter has not been made.

It must have existed in Nova Scotia, if at all. But at the same time its absence from Greenland and Labrador, where, in accordance with what we know of the geographical distribution of animals, it ought to occur along with *L. palliata* if it is indigenous; the extreme improbability of its remaining in such a small area without spreading, with causes in existence tending to carry it from a less favorable to a more favorable habitat; and the impossibility of the species remaining isolated from the parent stock in England for an indefinitely long time, and yet in spite of quite a differently conditioned habitat remaining specifically identical with it, all of these facts tend to show that it did not exist even in Nova Scotia. Is not the conclusion warranted then, that *Littorina litorea* is not indigenous to America, but has been recently and artificially introduced from Europe?

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